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THE HISTORY, COMPARATIVE ANATOMY AND EVOLUTION OF THE ARAUCARIOXYLON TYPE.

By Edward C. Jeffrey.

CONTRIBUTIONS FROM THE PHANEROGAMIC LABORATORIES OF HARVARD UNIVERSITY. NO. 55.

THE HISTORY, COMPARATIVE ANATOMY AND EVOLUTION OF THE ARAUCARIOXYLON TYPE.

By Edward C. Jeffrey.

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Part I.

Fossil woods of the Araucarioxylon type are extremely abundant in the Mesozoic deposits. The only living conifers with wood of this type are confined to the Eastern tropical region, to Australasia and to South America and are all included under the two genera Agathis and Araucaria. As a consequence of their habit, which differs from that of all living Conifers, except certain of the Podocarpineae, and of the organization of their woody tissues, the Araucarian Conifers have been most commonly referred to affinities with the Cordaitales, an important gymnospermous group of the Paleozoic. As will be shown in connection with the present investigations, the importance of these features of resemblance has apparently been much exaggerated. The association with the Cordaitales carries with it the implication, that the Araucariineae are either the ancestors of the other existing coniferous tribes, as is quite commonly held, or else that they constitute a separate line of descent, distinct from the ancestral stock of the remaining Conifers, as has been maintained in recent years by Seward and Penhallow. It is obviously a matter of considerable importance to clear up the affinities of the Araucarian stock, not only from the standpoint of its particular origin; but on account of the light thus to be thrown on the vexed subject of evolutionary processes as a whole by reason of the abundant display of the group during so long a period of geological time. The present writer has devoted nearly ten years to the procuring of material of Araucarian Conifers living and extinct and to the developmental, experimental and comparative anatomical investigation of their various organs and tissues.

It cannot be too strongly emphasized in connection with the present work, that general principles in biology are either of universal validity or of little scientific value, and that they cannot in certain cases be admitted and in others denied. There can be little doubt moreover that not a little of the existing reaction against the hypothesis of evolution, is the result of a failure on the part of biologists to apply evolutionary principles clearly, consistently and logically to the elucidation of their investigations, even if only from the standpoint of a working hypothesis. It seems clear that either there are generally valid biological principles, as there are commonly accepted principles in chemistry, physics and the other cognate sciences, or that biology has either not yet reached the scientific stage of development or has ceased to exist on the scientific footing. There appears to be no reason to adopt either of the latter alternatives. . Darwin in the prolegomena to his Origin of Species, emphasized the importance of the data supplied by development, history, comparative anatomy and geographical distribution in connection with the study of evolutionary processes in living beings. Since Darwin's time experimental methods have come largely into the foreground and there can be little doubt that evidence derived from this source, especially when controlled by an adequate knowledge of the geological history of beings now living, is of paramount importance. It is proposed in the series of articles of which this is the first, to discuss the origin, affinities and evolution of the Araucarian Conifers, so far as appears profitable, along all the important lines of investigation, indicated above.

It will be convenient here to define the Araucarioxylon type of wood. In the mature secondary wood of the trunk in the living Araucaria and Agathis, we find certain peculiarities, which are taken together unique among living conifers. The tracheids in these two genera are characterized by the presence of pits, which are closely approximated and flattened, or where they occur in two or more rows, alternating in their arrangement and polygonal in their form. The wood of the Araucarian type in respect to its pitting resembles in a marked degree that of the Cordaitales. The remaining tribes of existing Conifers possess a type of tracheary pitting in which the pores are rarely or never closely contiguous and when in several rows are opposite and not alternating. The pits in this type too are often separated by cellulose bars running transversely across the lignified walls of the tracheids and imbedded in their substance. These bars of Sanio are absent in the Araucarian conifers.[1] They should not be confused

[1] Gerry, Eloise, The Distribution of the Bars of Sanio in the Coniferales, Ann. Botany, **24**, p. 231.

with the trabeculae of Sanio, lignified processes, crossing the lumen of the tracheids, common to the Gnetales, Coniferales and a few Angiosperms. Another feature of the Araucarioxylon type is the usual absence of wood parenchyma and the smooth walled character of the ray cells. The last two features are less typical than the ones mentioned above since they are shared to a considerable extent by the woods of the remaining tribes of Coniferales. The last character has had recently assigned to it an apparently exaggerated importance.[2] Gothan has recently referred woods, which are strikingly Araucarian in the aggregate of their characteristics, to abietineous affinities on account of their strongly pitted rays, apparently losing sight of the fact that pitted rays occur commonly or sporadically in all the tribes of Conifers. The present article is to be devoted to the historical, comparative anatomical and experimental study of the rays and wood parenchyma in the Araucarian Conifers.

Beginning with the historical aspect, Figure *a*, Plate **1**, shows the character of the pitting in the tracheids in an Araucarian wood of the Upper Jurassic, to be described in detail on another occasion. The pits are numerous and in several rows, with the marked alternation, characteristic of the Araucarioxylon type. They are not however as closely approximated as is the case with the pits in the tracheids of the adult wood of the living genera Araucaria and Agathis. Figure *b*, Plate **1**, illustrates the ray structure in the same wood. It is clear that the cells of the ray, in contact with one another are very strongly pitted, exactly for example as is commonly the case in the rays of the Abietineae. On account of the pitting of the rays in woods of this type from the Upper Jurassic of King Carl's Land [3] and of the island of Spitzbergen [4] Gothan has recently referred them to abietineous affinities. It is to be pointed out in this connection that Seward has considered woods of a similar type from the Upper Lias of Yorkshire in England [5] to belong to the Araucarian conifers. Moreover Lignier more recently has described woods of a similar or nearly similar horizon, as likewise of Araucarian affinities.[6] About the same time

2 Gothan, Zur Anatomie lebender u. fossiler Gymnospermen-Hoelzer; Abh. d. Koenig. Preuss. geolog. Landesanstalt; Neue Folge, Heft 44, Berlin (1903).

3 Gothan, Fossilen Hoelzer von Koenig Karl's Land, Kung Svensk. Vetenskap. Handlingar, Bd. 42, No. 10.

4 Gothan, Fossilen Holzreste von Spitzbergen, Kung. Svensk. Handlingar, Bd. 45, No. 8.

5 Cat. of Mesozoic Plant, Brit. Museum, Jurassic Flora, Pt. 2, pp. 56, 57, pls. 6, 7, London (1904).

6 O. Lignier, Végétaux Fossiles de Normandie, IV. Bois Divers (Ire. Série), Caen (1907).

the present writer described woods of a similar type with a similar expression of affinities from a horizon, variously estimated from Middle to Lower Cretaceous, displayed at Kreischerville, Staten Island, N. Y.[7] It will be noted that the weight of opinion is against Gothan, in the matter of the reference of woods Araucarian in other respects, which have the strongly pitted rays of the Abietineae, to affinities with that tribe of Conifers, since Professor Seward, Professor Lignier and the writer agree in retaining them with the Araucariineae. Since a correct scientific verdict, however, does not depend on majorities, it will be well to investigate the matter from other standpoints.

A fundamental doctrine of Biology, owing its origin primarily to the deductive methods of the philosopher rather than to the more severe inductive procedure of the sciences, but since strongly confirmed by purely inductive data, is the doctrine of recapitulation. While it is undoubtedly the case that the seedlings and sporelings of the higher plants vouch in the strongest way for the validity of the recapitulation hypothesis, we have on the vegetable side corollaries to that doctrine, not illustrated as a rule by animals. There are organs of the plant for example, even more strongly retentive of ancestral characters than the seedling stem. Perhaps the most conservative organ is the root, which varies so little in its fundamental organization throughout the vascular plants, that one formula will represent the organization of all roots. In the case of the Gymnosperms and other typically coniferous groups, the axis of the cone has likewise been found to be strongly retentive of features which have disappeared entirely in the vegetative stem. Figure *c*, Plate 1, shows the inner region of the woody cylinder of the cone of *Agathis australis*, in transverse section. It is clear that the cells of the wood rays are in contrast to the typical condition for living Araucarian Conifers, very strongly thickened and even in this unfavorable plane of section, obviously pitted. We have in other words a condition present like that found in certain Jurassic and Lower Cretaceous woods which have been referred by the majority of paleobotamists, who have specially investigated them, to Araucarian affinities. Gothan however as pointed out above, places them on account of their thickened and strongly pitted ray-cells among the Abietineae. Figure *d*, Plate 1, shows a vertical section of one of the rays of the cone of *Agathis australis*, from which the contents have been removed in order that the sculpture

[7] Araucariopitys, a new genus of Araucarians, Bot. Gaz., **44**, 1–15, pls. 27–30, (1907).

of the cell walls might stand out more clearly. It is obvious from the pitting of the tracheids seen on the left of the figure, that we have to do with araucarian wood, since the pits are alternating. The ray cells very strongly pitted on all their walls, towards the right of the figure, towards the left thin out and assume the ordinary Araucarian type. Figure *e*, Plate **1**, shows part of the foregoing very highly magnified. The nature and abundance of the pits are now very clearly seen.

Not only does the cone of *Agathis australis*, clearly show the strongly pitted rays, which are found in the Jurassic and Lower Cretaceous woods, referred by the majority of recent investigators, to araucarian. affinities, but we find that the Mesozoic type of ray may be recalled by injuries to the root and the *seedling* stem. Figure *f*, Plate **1**, illustrates the modification of ray structure which frequently occurs in the old roots of Agathis australis as the result of injury. The cells in this case too are much thickened and strongly pitted. The normal seedling rays of *A. australis* have not been observed to show pitting or thickening on their terminal or horizontal walls in any case. The mature stem rarely shows reversion in ray structure to the earlier Mesozoic type as a result of injury. *Agathis australis* merely furnishes a good illustration of a condition of affairs in normal and traumatic anatomy, which so far as it goes, in accordance with accepted biological principles, vouches for the descent of the existing representatives of the Araucarian stock from ancestors in the Mesozoic, which possessed rays like those of living as well as extinct representatives of the Abietineae. Similar facts have been observed in other cases not only in the genus Agathis but also in Araucaria. It appears unnecessary to enlarge upon these at the present time.

Attention may now be given advantageously to the question of wood parenchyma in the Araucariineae. As is well known the Cordaitales, from which perhaps the majority of botanists at the present time directly derive the Araucarian Conifers, were characterized by the complete absence of wood parenchyma. The living species of Agathis and Araucaria, manifest this condition likewise in the normal mature wood of the stem and thus present *prima facie* evidence of close affinity with Cordaitales and other ancient Gymnosperms. Here again we may turn with advantage to the historical evidence and then to comparative anatomical and experimental data in the living representatives of the Araucarian stock, Figure *a*, Plate **2**, shows a longitudinal section of an Araucarian wood from the Raritan Cretaceous of Kreischerville, Staten Island, N. Y. Certain dark

longitudinal stripes are to be noticed particularly to the right of the center of the figure. These represent resiniferous parenchyma. Figure *d*, Plate **2**, shows a portion of the last figure more highly magnified, to make clear the transverse partitions separating the resiniferous elements from one another. Figure *b*, Plate **2**, shows the same wood in transverse section, the dark spots indicating the presence of the resiniferous cells. Figure *c*, Plate **2**, shows a section of the same wood near the pith, making it clear that we have to do with the stem wood of an extinct araucarian conifer. The resiniferous elements can be seen as in the preceding figure scattered throughout the wood. The writer has had the opportunity of examining a number of araucarian woods from the Raritan Cretaceous of the Eastern United States and has found in all true Araucarioxyla an abundance of wood parenchyma. In this respect they present a marked contrast to the normal stem wood of the living Agathis and Araucaria, although resembling them to a striking degree in other respects.

Let us now turn our attention to the conservative organs of the living genera. Figure *e*, Plate 2, illustrates the structure of an old root of *Agathis australis*, near the center. It is to be observed that the wood is thickly sown with parenchyma cells. These, it may be added are most abundant near the center of the root and die out progressively as the outer annual rings of the older root are reached, unless recalled by injury, as is noted below. Figure *a*, Plate **3**, shows a longitudinal section of the same root, making it clear that we have really to do with resin cells and not merely with tracheids filled with a resinous or mucilaginous contents such as are not infrequent in coniferous woods of varied affinities. Resin cells are extremely common in the first formed annual rings of the root in the genus Agathis and likewise occur to a less degree in the root organs of Araucaria. In certain species of Agathis, they likewise are found in *the first annual ring of the stem*. This condition may be illustrated by *A. australis* and *A. Bidwillii*, which represent as nearly as possible the extremes of affinity within the genus. Figure *b*, Plate **3**, illustrates the mode of occurrence of parenchyma in the first year's growth of *A. Bidwillii*. The dark spots are parenchyma cells. Figure *c*, Plate **3**, shows a longitudinal section of the same species. On the left is seen the protoxylem and a little to the right of the center, a row of parenchymatous elements, still retaining their protoplasmic contents. Figure *d*, Plate **3**, shows the same conditions in the first annual ring of *A. australis*. Here the parenchyma tends to occupy the face of the summer wood, in the first yearly increment, thus resembling the conditions

found by Gothan in certain araucarian woods from King Carl's Land apparently wrongly referred by him to abietineous affinities.[8] Figure *e*, Plate **3**, is a longitudinal section of the same species, illustrating the vertical distribution of the wood parenchyma. Seldom or never does parenchyma make its appearance in the normal wood of outer annual rings. At this point it is convenient to record another feature of interest. Through the kindness of Messrs. Eames and Sinnott, Sheldon fellows of Harvard University, who have recently spent a year in the investigation of the coniferous flora of the Australasian region, the writer has been supplied with seedlings of the genera Agathis and Araucaria. It was found on investigation that in the case of Agathis there was usually no wood parenchyma in the first annual ring in the seedling until it had reached a considerable size. In fact it is only in the vigorous branches that bear cones that the parenchymatous elements appear in any abundance. The recapitulationary phenomena in the case of wood parenchyma are accordingly delayed until the plant has reached a certain vigor, thus presenting an exact homologue with the conditions found for example in certain of the Abietineae, which are normally without resin canals in the wood [9] and in *Sequoia gigantea*.[10] Here the resin canals, so characteristic of the pine-like Abietineae, occur in the first annual ring of vigorous vegetative shoots and in a few cases only in the axis of the cone. The evidence in the case of the genus Sequoia and in the Abieteae, has been accepted by other investigators who have given special attention to the Conifers, as a clear indication that both the Abieteae and Sequoia have come from pine-like ancestors.[11] Mr. Thomson's views in this respect are particularly significant as his attitude in regard to the affinity of the Araucarian conifers is diametrically opposed to that of the present writer. As will be pointed out later, the admission of the validity of certain general principles in the case of certain coniferous tribes, logically implies their application to the whole series. We find then this feature of accord between recapitulationary phenomena in for example Abies and Sequoia on the one hand and Agathis on the

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8 Gothan, Die Fossilen Hoelzer von Koenig Karl's Land, Kung. Svensk, Vetenskab. Handlingar, Bd. 42, No. 10.

9 Jeffrey, Comp. Anat. of the Coniferales, No. 2. The Abietineae, Mem. Boston Soc. Nat. Hist., **6**, pp. i–37, pls. 1–7 (1904).

10 Comp. Anat. Coniferales, No. 1, The Genus Sequoia, Mem. Bost. Soc. Nat. Hist., **5** (1903).

11 Coulter and Chamberlain, Morphology of Gymnosperms, Chicago (1911), and Thomson, R. B., Megasporophyll of Saxegothea and Microcachrys, Bot. Gazette, **47** (1909).

other, that the resin canals in the case of the former and the resiniferous parenchyma in the case of the latter, do not appear in the first annual ring of the seedlings but only in the first annual increment of older and more vigorous axes. In the case of Agathis it is clear from the fossil data, that we actually have a harking back to ancestral phenomena, presented in the extinct forms as shown above. In Abies and Sequoia we can only infer that their ancestors had resin canals in accordance with accepted principles of biological science. It seems clear also in both types of illustration, that we have in the case of the living representatives, to do with reduction phenomena. The fact that Abies and Sequoia on the one hand and Agathis on the other hand are degenerate descendants of stocks once more vigorous and richly endowed, doubtless furnishes the explanation of why the recapitulationary phenomena in connection with the first annual ring make their appearance not in the seedling; but only after the plant has attained the reproductive age.

Figure *f*, Plate **3**, illustrates the conditions found in connection with the parenchyma of a wounded root of *Agathis australis*. It is to be noticed that most of the parenchymatous cells are thick-walled and in some instances strongly pitted. This figure is to be compared with Figure *c*, Plate **1**, which shows the normal condition of the cone axis. Here both the rays and parenchyma are thick-walled on the side nearer the pith. In the case of *A. australis* the adult stem, when injured, in contrast to the root does not form thick-walled wood parenchyma but only thin walled elements. That this is the case is demonstrated by Figures *a* and *b*, Plate **4**, which show the injured stem wood of *A. australis* in transverse and longitudinal section. Thin-walled parenchyma can be seen in each case.

Figures *c* and *d*, Plate **4**, show the transverse and longitudinal views of the heart wood of *A. australis*, illustrating the presence of resinous exudations in the tracheids of the wood immediately adjacent to the rays. In the longitudinal view the relation of the exudation to the ray cells is particularly well seen. Penhallow has compared these transverse septa, resulting from substances poured out by the ray cells into the tracheids with the trabeculae of Sanio. They have in reality of course nothing to do with these structures.[12] Lignier has described the thickening up of the tracheids adjacent to the rays in certain Araucarian woods from the French Jurassic. It seems entirely probable that he has mistaken resin filled tracheids for thick-walled

12 Penhallow, North American Gymnosperms, Boston (1907), pp. 53–58.

ones, as a result of the bad condition of preservation of his material.[13] Figures *e* and *f*, Plate 4, make this probability practically a certainty. Figure *e* illustrates the transverse view of *Araucarioylon noveboracense* from the Raritan Cretaceous of Staten Island.[14] The tracheids in contact with the rays are apparently distinguished by their very thick walls. Figure *f*, which represents a longitudinal view of the same piece of lignite, makes it clear that the apparently thick walled tracheids are in reality only tracheids more or less occupied by a plugging exudation from the rays.

Although a general statement as to the inferences to be drawn from the series of articles, of which this is the first, will appropriately appear in connection with the last of the series, it is apposite and necessary to point out the particular conclusions to be derived from the observations recorded here. It is clear that there are certain definite structural relations between the Araucarian woods now in existence and those no longer living. In general the structural features of the Mesozoic Araucarioxyla are strongly retained in the cone axis, and the root of living species. They are less strongly retained in the vegetative stem. In the case of the latter, ancestral features may reappear in the first annual ring of axes of unusual vigor or as a result of injury. Injuries to the root result in the recall of more ancient features than those which can traumatically be recalled in the stem. Further it is clear that the comparative developmental and experimental study of living Araucarian conifers is of the greatest value and significance in connection with the accurate diagnosis of fossil forms. A comparison of living with extinct forms, so far as the points considered in this article are involved, shows that certain Mesozoic woods, which have been referred by Seward, Lignier and the present writer to the Araucariineae, in reality have that systematic affinity and are not as has been recently suggested by Gothan, the woods of Abietineous Conifers.

Conclusions.

1. The ancestors of Araucaria and Agathis were characterized by the possession of wood parenchyma.
2. They likewise had strongly pitted rays.
3. The possession of these two features is quite inconsistent with their derivation from Cordaitean ancestry.

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13 *Op. cit.*, pl. 17.

14 Hollick and Jeffrey, Cret. Coniferous Remains, Staten Island, Mem. N. Y. Bot. Garden, **3**, pl. 21.

4. Certain woods from the Jurassic and Lower Cretaceous, possessing at once araucarian pitting, of the tracheids, abundantly developed wood parenchyma and strongly pitted medullary rays are in reality aruacarian in their affinities and not abietineous as has recently been asserted by Gothan on the insufficient basis of their ray structure.

5. The characteristic features of Mesozoic araucarian woods are retained to a large degree in the wood of cone axis, root and first annual ring of vigorous branches of living representatives of the Araucariineae.

6. They may be recalled by experimental means particularly in the root and the seedling stem.

PLATE 1.

Fig. *a*. Radial view of an undescribed wood from the Lias of Yorkshire, England, showing the Araucarian type of pitting. × 100.

Fig. *b*. Radial view of the wood of the same showing pitted character of the medullary ray × 100.

Fig. *c*. Transverse section of the wood of the cone-axis of *Agathis australis*, showing the strong normal pitting of the ray cells near the pith. × 100.

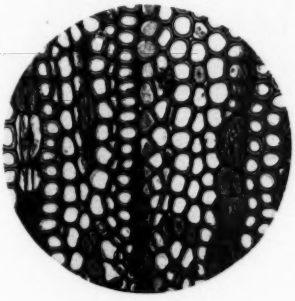
Fig. *d*. Radial section of the same showing character of the tracheids and the ray cells. × 100.

Fig. *e*. Part of the same. × 300.

Fig. *f*. Injured wood of the root of the same in transverse section, showing the thick-walled, strongly pitted ray cells formed traumatically. × 100.

a

b



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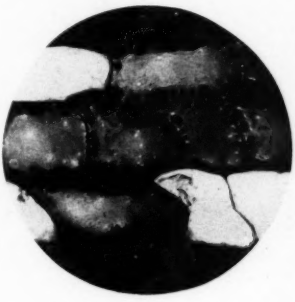

e

f

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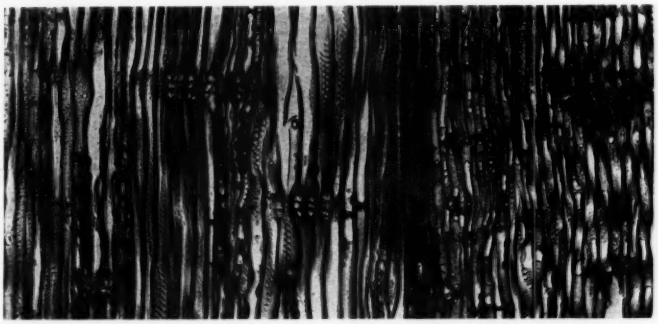
PLATE 2.

Fig. *a*. Radial view of the wood of *Araucarioxylon noveboracense*. × 50.
Fig. *b*. Transverse section of the same. × 40.
Fig. *c*. Transverse section of the same near the pith. × 40.
Fig. *d*. Long radial section of the same. × 100.
Fig. *e*. Transverse section of the wood of the root of *Agathis australis*. × 40.



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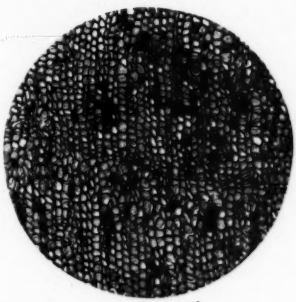

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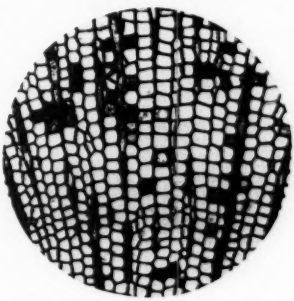

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PLATE 3.

Fig. *a*. Radial section of the same. × 40.

Fig. *b*. Transverse section through first annual ring of stem of *Agathis Bidwillii*, showing resin cells. × 40.

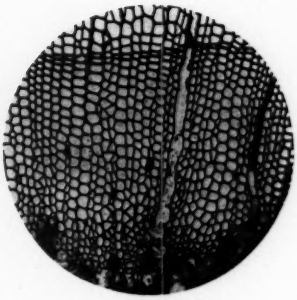
Fig. *c*. Longitudinal section of the same. × 40.

Fig. *d*. Transverse section of old stem of *Agathis australis*, showing first annual ring. × 60.

Fig. *e*. Radial section of the same. × 60.

Fig. *f*. Transverse section of root wood of *Agathis*, showing both pitted and thin walled parenchyma. × 100.

a



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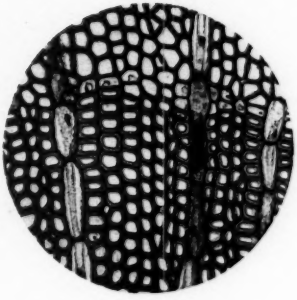

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HELIOTYPE CO., BOSTON

PLATE 4.

Fig. *a*. Wounded wood of the stem of *Agathis australis* in transverse section, showing the return of the ancestral wood parenchyma as the result of injury. × 100.

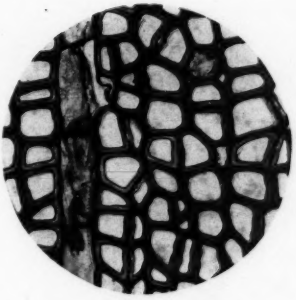
Fig. *b*. The same in radial section. × 100.

Fig. *c*. Wood of *Agathis australis* (normal) in transverse section, showing plugging of tracheids in proximity to the rays. × 40.

Fig. *d*. The same in tangential longitudinal section, showing relation of plugs to the ray cells. × 40.

Fig. *e*. Transverse section of the wood of *Araucarioxylon noveboracense*, for comparison with Figure *c*. × 40.

Fig. *f*. Tangential section of the same for comparison with Figure *d*. × 40.



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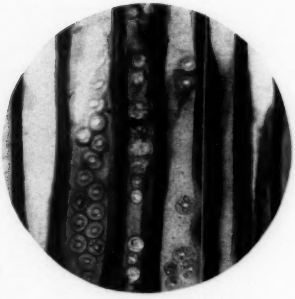

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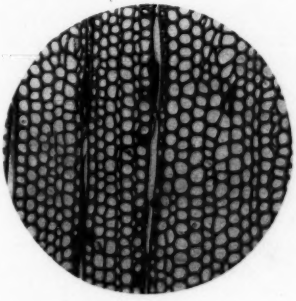

c

d

e

f

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By Edward C. Jeffrey.

Part II.

In the first article of the present series the structure of the rays and the parenchyma of woods of Araucarian affinities, was considered. In the present one the characteristic features of the tracheids and the nature of the pitting will be particularly discussed. The pitting of the tracheary elements in the Araucarian Conifers has been considered by practically all writers as an infallible criterion for the diagnosis of their woods as fossils. It is unnecessary to enter upon this matter in detail as the literature on the subject has quite recently been admirably summarized by Gothan.[15] It is universally assumed that crowded radial pits on the tracheid walls either flattened by mutual contact, if the pores are uniseriate, or of somewhat polygonal outline in case the pits are in several rows, indicate Araucarian affinities. Recently however a tendency to question the universal validity of the Araucarian type of tracheary pitting as an indication of Araucarian affinities has made itself felt. On the one hand it has been maintained that woods with typical Araucarian pitting in reality were referable to the Abietineae on the assumed more important character of their ray structure.[16] On the other it has been maintained that woods without typical Araucarian pitting in reality belonged, in consideration of the sum of their characters to the Araucarian Conifers.[17] The

15 Zur Anatomie lebender u. fossiler Gymnospermen-Hölzer, Berlin (1905).

16 Gothan, Die Fossilen Hölzer von König Karl's Land, Kung. Svensk. Handlingar, Bd. 42, and Gothan, Die Fossilen Hoelzreste von Spitzbergen, Kung. Svensk. Vetenskap Handlingar, Bd. 45.

17 Gerry, Eloise, Distribution of the bars of Sanio in the Conifers. Ann. Bot. **24** (1910); Sinnott, E. W., Paracedroxylon, a new type of Araucarian wood, Rhodora, **11**;Jeffrey, E. C., The Affinities of *Geinitzia gracillima*, Bot. Gazette, **50**.

question of the value of Araucarian pitting as an indication of Araucarian affinities is all the more important because it likewise has been made to involve the relationship of the Araucarian Conifers with the Cordaitales of the Paleozoic, which as regards their pitting strongly resemble the conditions typical of the wood of the living Agathis and Araucaria. Still another important question arises in connection with certain features of organization of the Araucarian tracheid as compared with that found in other Conifers. It has been pointed out by Miss Gerry [18] that the Araucarian Conifers both living and extinct are without the horizontal cellulose bands, between the radial bordered pits, characteristic of all other Conifers. This feature has an added importance from the fact that a similar feature is likewise characteristic of the wood of the Cordaitean gymnosperms. It is the purpose of the present article to deal with these features of the Coniferous tracheids in regard to their value as indications of tribal relationship and evolutional sequence in the Coniferales.

It will be convenient to begin with the subject of Araucarian pitting. Figure *a*, Plate 5, shows the crowded alternating arrangement of the tracheary pores, which is regarded as typically Araucarian. The illustration is taken from the wood of *Araucarioxylon, noveboracense*, from the Raritan Cretaceous of Kreischerville, Staten Island, N. Y.[19] Figure *b*, Plate 5, illustrates the arrangement and propinquity of the radial bordered pits in the *first annual ring* of the same type of lignite. The absence of approximation and consequent flattening of the bordered pits is very apparent. An examination of a considerable number of true Araucarioxyla from the American Cretaceous has led the writer to the general conclusion that no matter how typical the Araucarian arrangement of the pits may be in the mature wood, that in the first annual ring of the stem one always finds a marked tendency to the rounded and well spaced pits which are typical of the wood of the Abietineae and allied Conifers.

Further in connection with recent investigations on woods of the American and European Mesozoic, numerous instances have been described, presenting to a greater or less degree Araucarian characteristics, but with a marked departure from the Araucarian type of pitting This is notably the case, for example, with the recently established genus Brachyoylon.[20]

An even more striking illustration is supplied by the genus Para-

[18] *Op. cit.* [19] *Op. cit.*

[20] Hollick and Jeffrey, Cretaceous Coniferous Remains from Kreischerville, Mem. N. Y., Bot. Garden, No. III.

cedroxylon recently described by Sinnott.[21] Perhaps the most conspicuous illustrations of this condition are supplied by Araucariopitys[22] and the so called *Cedroxylon transiens* of Gothan.[23] Here not only does the pitting depart largely from the Araucarian type, but the wood is likewise particularized by strongly pitted rays resembling those of the Abietineae. It is clear from the facts and citations of facts here assembled, that in the Mesozoic there were woods which either had the Araucarian type of pitting very imperfectly developed or if well displayed in the adult wood, not found to be present in the first annual ring. It may be stated in anticipation of conclusions to be drawn later, that it follows that Araucarian pitting was not a characteristic of the primitive stock from which the Araucariineae of to-day and their nearest relatives in the Mesozoic, were derived.

The conditions in the living genera of the Araucariineae as regards pitting, may now advantageously be considered. Figure *c*, Plate **5**, shows the appearance of a radial section of the wood in an old seedling stem of *Agathis australis*, perhaps the most highly specialized species of the genus now in existence. The pits are obviously much crowded and when in a single row strongly flattened, or when multiseriate somewhat polygonal in shape. Exactly similar conditions are found in the case of the wood of species of Araucaria, and as a consequence it is not necessary to illustrate by a figure the wood structure in that genus. Figure *d*, Plate **5**, shows a radial section of the wood at the base of the seedling stem of *Agathis australis*. Here the pits are obviously not crowded or flattened by mutual contact. This condition is found for several inches above the ground in the seedling stem and for a great number of annual rings outwards, as many for example as fifteen. In the main root of the seedling similar conditions are found to a considerable depth but in the secondary roots, the pitting becomes typically Araucarian, with the very many rows of pits, characteristic of root wood in general. In the seedling stem of *Araucaria Bidwillii*, *A. imbricata* and *A. Cookii*, very similar conditions were found, to a less marked degree and lower down in the stem, rather in its hypocotyledonary than its epicotyledonary region. It is an interesting fact that in the seedling stem of the living genera of the Araucarian Conifers, we find perpetuated the type of pitting charcteristic of Brachyoxylon,[24] Araucariopitys,[25] Paracedroxylon,[26] *Cedroxylon transiens*[27] from various levels of the Mesozoic. Here we have illustrated in a

21 *Op. cit.*
22 Jeffrey, Bot. Gazette, **44** (1907).
23 *Op. cit.*
24 *Op. cit.*
25 *Op. cit.*
26 *Op. cit.*
27 *Op. cit.*

remarkable way the validity of the doctrine of recapitulation, in accordance with which the young individuals of living species may pass through in their earlier stages of development the condition found typically in their extinct ancestors of more or less remote geological time.

The first annual ring of the living species of Agathis and Araucaria, unlike the Araucarian woods of the Araucarioxylon type, from the American Cretaceous, shows only slightly and often sporadically the departure from Araucarian pitting characteristic of Brachyoxylon, etc. Not more than two or three tracheids next the protoxylem in the most favorable cases illustrate this feature. In this respect the existing woods of the Araucarian type show themselves, as might be expected, less retentive of ancestral characters than is the case with the similar woods from the Cretaceous. In the case of the normal type of Araucarian wood, not only the approximation but also the alternation of the radial pits of the tracheids are characteristic features. Figure *e*, Plate 5, shows under a comparatively low magnification, the structure of the tracheids adjoining the protoxylem in the cone of *Araucaria Bidwillii*. It is easy to make out that the pits in the tracheary elements of the secondary wood nearest the scalariform elements of the protoxylem, are arranged for the most part in opposite pairs. Moreover even with the low magnification employed it is clear that the pits in question are not flattened by mutual, approximation. In other words we have the conditions present, so far as the radial pitting is concerned, which are typical of the wood of the Abietineae and other tribes of Conifers. Farther away from the protoxylem the pitting passes into the typical araucarian condition. Figure *f*, Plate 5, shows a part of the last more highly magnified. On one side the tracheids still retain some indications of the spiral and reticulate sculpture of the protoxylem. On the other tracheids of the secondary wood have made their appearance. They are characterized, however, by a distinctly non-Araucarian arrangement of the pits and by other remarkable and important features. The pits are separated from each other by appreciable intervals. The most remarkable feature, however, shown by the tracheids in this region is the presence of dark discontinuous stripes crossing the tracheids transversely between the pits. These dark stripes in the photograph often fork at the ends and represent cellulose bands in the substance of the tracheid walls. They are in fact typical bars of Sanio (not to be confused with the 'Balken' or trabeculae of Sanio, which are a very different thing), found normally in all the tribes of Conifers except the Araucariineae.

Before passing to the consideration of the significance of these structural features of the wood of the cone in *Araucaria Bidwillii*, it will be well to examine them more particularly in this species and discover their occurrence and development in other species of Araucaria as well as in species of the allied genus Agathis.

Figure *a*, Plate **6**, illustrates the conditions presented in another photograph of a radial section of the wood in *Araucaria Bidwillii*. Here although the magnification is not great the bars of Sanio stand out with great clearness between the pits, which on the whole tend more in their arrangement to the typical Araucarian condition of alternation than in the figures described above. The tracheids are bounded above and below by wood rays, showing that although they lie near the primary wood they are typical elements of the secondary xylem. Figure *b*, Plate **6**, shows a very highly magnified view of parts of three tracheids of the secondary wood in proximity to the primary xylem. Here it is possible to distinguish the bars of Sanio with great clearness. They are as a rule, invariably in the figure under discussion, not continuous across the tracheid, but subtend usually the breadth of a single pit. The forking of the cellulose bars at the ends can be clearly made out.

Figure *c*, Plate **6**, shows the conditions in the tracheids of the secondary wood, adjacent to the primary xylem in *Araucaria imbricata*, very highly magnified. On one side of the figure can be seen a spirally sculptured element of the primary xylem. On the other, one tracheid in particular shows clear bars of Sanio. In *Araucaria imbricata* which, as will be shown later, as a result of the consideration of a number of lines of evidence is among the least primitive species of the genus, the tracheids showing well spaced pits and clearly discernible bars of Sanio are very few in number. *Araucaria Cookii* and *Araucaria Rulei* were likewise examined, with results intermediate between those found in *A. Bidwillii* and *A. imbricata* which appear in these as in other respects to represent the extreme conditions found in the genus.

For comparison an illustration of the conditions in the mature secondary wood of *Pinus strobus* is shown in Figure *d*, Plate **6**. Here the cellulose bars of Sanio are very distinct between the uni- or bi-seriate pits. The pits where they are in two rows are opposite. The occasional forking of the bars at the ends can likewise be made out. The pits are well spaced and rounded.

Figure *e*, Plate **6**, shows a tracheid wall of *Araucaria Bidwillii* in tangential section. That the plane of section is in reality tangential

and that the element belongs to the secondary wood is vouched for by the presence, on the right and left, of cells of the wood rays in transverse section. The dark transverse sections of the bars of Sanio, embedded in the substance of the lignified tracheid wall, between the radial pits, are easily distinguished. Figure *f*, Plate 6, illustrates the conditions observable in the ordinary secondary wood of the vegetative axis. Obviously the pits as seen in profile are here in close contact and are not separated by bars of Sanio.

The stem of the seedling and the first annual ring of the adult branches of various species of Araucaria, were examined in the region of the primary xylem for the presence of bars of Sanio. Where any evidence of their existence was apparent, however, they were extremely indistinct and ghostly and very evanescent. The same conditions were observed in the root. In accordance with the now widely accepted dictum of comparative anatomy that the leaf trace is very apt to perpetuate ancestral conditions, the foliar traces of several species of Araucaria were investigated, but on account mainly of the small size of the tracheary elements, it was difficult to make out the presence of bars of Sanio, with any distinctness, although their existence in these regions was indicated.

The absence of bars of Sanio in the seedling, where the pits are often widely separated from one another, is of particular significance, in view of the statement of Gothan, that their non-existence in Auracarian woods is to be explained by the close approximation of the pits. Obviously such an explanation will not hold in the case of the undoubtedly Araucarian wood of Araucarian seedlings.[28] It follows that woods from the Mesozoic which are without typical Araucarian pitting, can best be diagnosed as to their affinities not on the basis of their radial pitting or even their ray structure, but by the presence or absence of bars of Sanio, in well preserved material. Where the bars are present in the mature wood, we may certainly assume that the wood is not Araucarian. On the other hand, where the bars of Sanio are distinctly absent in well preserved Mesozoic woods, it may safely be concluded that they are of Araucarian affinites, no matter what may be the nature of their radial pitting or that of the cells of their rays.

In conclusion of the descriptive part of the present article, it is necessary to refer to the pitting and structure of the tracheids in the living genus Agathis. It has been found here, that even in the cone, the tracheids very quickly cease to show opposite pitting and the bars

[28] Gothan, Die fossilen Holzreste von Spitzbergen, Kung. Svensk. Vetenskap, Handlingar, Bd. 45.

of Sanio in all cases are shadowy and difficult to discern, although they can be made out by the eye of expectancy. *Agathis Bidwillii*, material of which was received from the Botanic Garden at Buitenzorg, Java, through the kindness of the late Dr. M. Treub, Director, proved in this respect to be most favorable. Even here, however, in the most favorable instances, the bars of Sanio are scarcely as well developed in the wood of the cone, as they are in the least favorable species of Araucaria, which has been examined and figured in the present connection, viz. *A. imbricata*. It does not seem necessary on that account to present illustrations of Agathis. *A. australis* shows bars of Sanio, less distinctly than any other species examined. No indication whatever of the existence of bars of Sanio has been found in the seedling of *A. australis*, although it has been examined in detail with considerable care.

Finally attempts were made to discover bars of Sanio in the region of the primary wood in species of Araucarioxylon. Here on account of the generally bad state of preservation of the material and also doubtless on account of the delicate nature of the bars in this region, even in living representatives of the Araucariineae, the results were entirely negative. It is well perhaps at this point to indicate the best method of demonstrating bars of Sanio in the wood of cones of living species of the Araucarian tribe. Haidenhain's hematoxylin was found most useful for bringing out the structure in question; but care must be taken to have both the hematoxylin solution and the iron alum solution perfectly fresh. The sections after being subjected to the action of the iron alum for ten or fifteen minutes are washed carefully and rapidly in three changes of distilled water. They are then allowed to remain in fresh distilled water for half an hour or more. Next they are treated for some time with hematoxylin solution of one fourth of one per cent strength. In this they remain for some time, up to half an hour. Unless the solutions are quite fresh they will become fatally overstained. After a washing or two in distilled water, the sections are transferred to a very dilute aqueous solution of safranin and allowed to remain for several hours or over night. If the process has been successfully carried out, the bars of Sanio will appear as intense blue transverse bands on the red background of the lignified cell wall of the tracheid. They are most easily seen nearer the ends of the tracheary elements, just as is the case in those coniferous woods where they are abundantly and normally present in the mature tissue.

It was considered that the appearances described above in connec-

tion with the obvious presence of bars of Sanio, might possibly be common to all secondary woods in the region of the primary xylem. Sections of the cone axis, the leaf-strands and roots of Cycas and Zamia were accordingly made and subjected to the same treatment. In no case was there any indication of the presence of horizontal bands of cellulose in the tracheids, between the radial bordered pits. Similar observations were made on the vegetative stem, the leaf strands and the reproductive axes of Ginkgo. Here as in the case of Cycas and Zamia, no bars of Sanio were seen in proximity to the primary wood. In fact in the reproductive axes and in the leaf strands no bars of Sanio were seen at all. In the vegetative stem, however, they appear late in the first annual ring, not in close proximity to the primary xylem. As is well known, Ginkgo resembles the mass of Conifers, in showing bars of Sanio clearly in its mature wood. Pinus, as probably the most primitive living representative of the Coniferales was likewise examined in this connection. Here the conditions closely resemble those found in Gingko, so far as the vegetative shoots are concerned, for the bars of Sanio make their appearance late and not in proximity to the primary wood. In the cone of *Pinus strobus*, bars of Sanio were not found at all. It is to be noted in connection with these results, as contrasted with those found in the case of the Araucarian Conifers that, there is clear evidence, so far as may be judged from the structure of the first annual ring, that Ginkgo and the genus Pinus are directly connected with the Cordaitean stock, in which bars of Sanio are absent and the pitting is alternating, while Agathis and Araucaria have obviously come from ancestors which, in accordance with accepted principles of comparative anatomy, had opposite pitting and bars of Sanio in their tracheids.

It seems to be quite clear so far as the particular features of wood structure, considered in the present article, are concerned, that far from the absence of bars of Sanio and the presence of alternating pitting in the woods of the Araucariineae, being an argument for their direct filiation with the Cordaitales, these features have clearly been secondarily acquired and the Araucarian stock primitively was characterized by the bars of Sanio and opposite pitting, which have been retained in the ligneous structure of all the other living tribes of the Coniferales. It is also quite clear from the fossil evidence that the loss of bars of Sanio, in the case of the Araucariineae, as well as the disappearance of the ancestral opposite pitting, took place at a period relatively remote. That this general inference is justified by a number of other equally important facts will be shown in the later articles.

Summary.

1. The characteristic pitting of the wood in Agathis and Araucaria, the Araucarioxylon type, is not ancestral but more recently acquired.

2. This conclusion is based on the structure of the first annual ring of the stem in Mesozoic Araucarioxyla. It is confirmed strongly by the seedling structure of the living genera and particularly by the anatomical structure of the wood of their cone axes.

3. The cellulose bars of Sanio, characteristic of the mature wood of all living genera of the Coniferales, except Agathis and Araucaria, are clearly present in the secondary tracheids adjacent to the primary wood of the cone axis in these two genera. They are absent in the seedling and cannot be clearly discerned in the leaf traces on account of the small size of the elements.

4. Since bars of Sanio do not occur in similar situations in Cycas and Ginkgo, it cannot be assumed that they are a feature of all gymnospermous woods in proximity to the primary xylem.

5. Since deviations of a significant nature in the pitting and structure of the tracheids occur in primitive regions of the Araucarian axes, which connect them with the remaining tribes of the Coniferales stock, it follows that so far as these features are concerned, the Araucarian Conifers are derived from the common coniferous plexus and are not directly articulated with the Cordaitales.

6. On the basis of comparative studies of the tracheids of the Araucariineae, they cannot be regarded as primitive representatives of the Coniferous order.

7. The real affinities of the Araucariineae can best be defined when all the evidence is considered in the concluding article of this series.

PLATE 5.

Fig. *a*. Radial section of the wood of *Araucarioxylon noveboracense*. × 200.

Fig. *b*. Radial section of wood in proximity to the protoxylem in the same. × 200.

Fig. *c*. Radial section of the wood of *Agathis australis*. × 200.

Fig. *d*. Radial section of the wood of the seedling of the same. × 300.

Fig. *e*. Radial section of the wood of the cone of *Araucaria Bidwillii*, in proximity to the protoxylem. × 60.

Fig. *f*. The same more highly magnified. × 200.

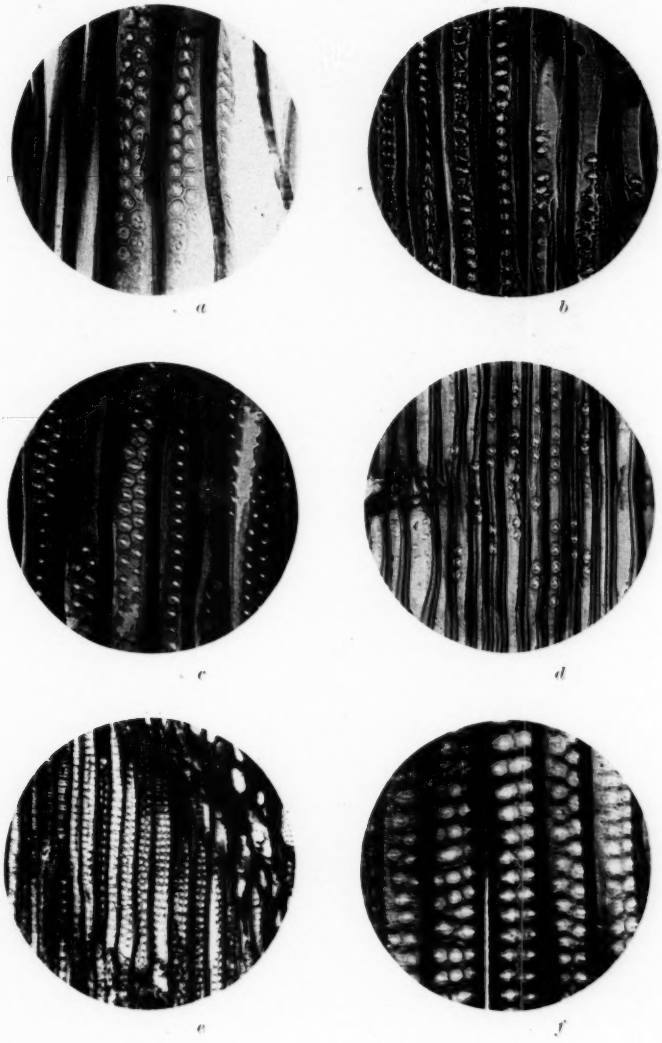

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PLATE 6.

Fig. *a*. Radial section of the same. × 100.

Fig. *b*. Another of the same. × 500.

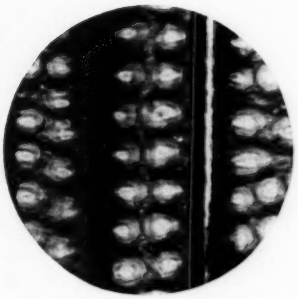
Fig. *c*. Radial section of the xylem of the cone of *Araucaria imbricata*, in proximity to the protoxylem. × 500.

Fig. *d*. Radial section of the wood of *Pinus strobus*. × 150.

Fig. *e*. Tangential section of the wood of the cone of *Araucaria Bidwillii*. × 500.

Fig. *f*. Tangential section of the wood of the vegetative stem of the same. × 300.

a



b

c

d

e

f

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THE HISTORY, COMPARATIVE ANATOMY AND EVOLUTION OF THE ARAUCARIOXYLON TYPE.

By Edward C. Jeffrey.

Part III.

The present article will be devoted to the consideration of resin canals in the wood of the Araucariineae, living and extinct. Some time ago the present writer in collaboration with Dr. Arthur Hollick [29] described the occurrence of resin canals as a result of injury in certain Araucarian woods from the Raritan Cretaceous of Kreischerville, Staten Island. Later a more complete study of this phenomenon was made, which included the consideration of more varied and abundant material from the Kreischerville deposits, as well as from the strata of similar age on the island of Martha's Vineyard and likewise from the much older Cretaceous Potomac deposits of Virginia. In this connection certain leafy twigs of Cretaceous Conifers were described in which the wood clearly showed the formation of resin canals as the result of injury. The twigs in question belonged to the well known Cretaceous genus Brachyphyllum, and for that reason the Araucarian type of wood, producing traumatic resin canals as a result of injury was named Brachyoxylon.[30] Still another type of Araucarian wood, forming traumatic resin canals was described by the present writer in 1907.[31] Here the canals were much more like the traumatic resin-canals of the Abietineae than has proved to be the case with any other araucarian woods, showing wound resin canals from the American

29 Cretaceous Coniferous Remains from Kreischerville, Mem. N. Y. Botanic Garden, No. III.

30 Jeffrey, E. C., Wound Reactions of Brachyphyllum, Ann. Botany, **20**, pp. 383–394, pls. 27, 28.

Hollick and Jeffrey, Cretaceous Coniferous Remains from Kreischerville, Mem. N. Y. Bot. Garden, No. III.

31 Araucariopitys, a new genus of Araucarians, Bot. Gazette, **44**, pp. 435–444.

Cretaceous. Araucariopitys, not only shows resin canals closely resembling those of the Abietineae, but likewise has wood rays, with strongly pitted cells very similar to those found in Abietineous woods. Previously Seward [32] had described woods of similar organization from the Lias (Upper Jurassic) of Yorkshire in England, under the appellation *Araucarioxylon Lindleyi*. These woods, which, so far as it is possible to judge from Professor Seward's description, belong partly to the Brachyoxylon and partly to the Araucariopitys type, were characterized by very well marked Araucarian pitting of the tracheids, accompanied by quite typical traumatic ligneous resin canals. Contemporaneously with the present writer's article on Araucariopitys, Gothan published a description of the fossil woods of the Upper Jurassic of King Carl's Land.[33] These are characterized by the presence of Araucarian pitting of the tracheids of the wood, by strongly pitted rays, resembling those of Abietineous woods, by, for the most part, terminal wood parenchyma, and often by the presence of traumatic resin canals. These woods are in general considered by Gothan to be intermediate between the Araucariineae and Abietineae and to indicate a derivation of the latter tribe from Araucarian ancestry. The writer agrees with Professor Seward in considering that the woods in question are distinctly on the Araucarian side in affinities. He is further of the opinion, which is apparently not shared by Professor Seward, that the Araucariineae on the basis of structure of Mesozoic woods are derived from the Abietineae and not *vice versa*, as is the opinion of the majority of competent investigators at the present time. Recently an overwhelming amount of evidence has been brought to light which appears to strongly support the present writer's contentions. More recently Gothan has published an extensive memoir on the fossil woods of the island of Spitzbergen, in which he described a number of interesting woods from the upper Jurassic (or Lower Cretaceous!!) resembling strongly those of King Carl's Land and in some instances presenting a still more striking combination of Abietineous and Araucarian characters.[34] The author in this memoir restates and emphasizes his opinion that the Abietineae have been derived from Araucarian ancestors.

Figure *a*, Plate **7**, shows the transverse section of a wounded speci-

32 Cat. Mesozoic Plants. Brit. Museum, Jurassic Plants, **2**, pps. 56–59. London (1904).

33 Kung. Svensk. Vetenskap. Handlingar, **42**, No. 10. Berlin (1908).

34 Kung. Svensk. Vetenskap. Handlingar, **45**, No. 8. Uppsala u. Stockholm (1910)

men of Brachyoxylon. On the left appears the wound parenchyma, which universally adjoins a wound in woody tissues. To the right of this appear certain somewhat compressed cavities in the wood, surrounded by cells filled with dark contents. The cavities in question are the traumatic resin canals, which are a feature of the Brachyoxylon type. Figure *b*, Plate 7, from the same specimen shows part of a row of traumatic resin canals farther away from the same wound. It is an interesting fact in woods, in which resin canals are either almost obsolete or may be recalled only by experimental means, that they occur in nearly continuous tangential rows. This for example is the case with the resin canals in the woods of species of the genus Sequoia and with the woods of the genera Abies, Cedrus, Tsuga and Pseudolarix of the Abieteae, which are admitted by those who have recently devoted special attention to the comparative anatomy of the Coniferales, to be descended from ancestors which possessed resin-canals abundantly and normally in their woods. It follows that the presence of traumatic resin-canals in close tangential rows in the genus Brachyoxylon is *prima facie* evidence that this type has come from an ancestry which possessed normal ligneous resin canals. This consideration alone enormously complicates the task of those who endeavor to derive the Abietineae from Araucarian ancestors, for they have to explain the presence of resin-canals in an obsolete and vestigial condition in forms, which they claim to be the direct ancestors of the pine-like Abietineae, in which the resin canals are highly developed. It is scarcely necessary to point out that this is a palpable logical contradiction. It is unnecessary to figure the longitudinal view of the traumatic resin canals in the wood of the Brachyoxylon type of Araucarian woods, since this subject has already been sufficiently dealt with in the articles by the present author cited above. It is well however to point out at this stage that Brachyoxylon has the type of ray which is characteristic of living representatives of the Araucarian stock, namely one in which the cells are without pits and thin walled, except where they are laterally in contact with the tracheids of the wood. The pitting in this type is often strikingly Araucarian and at the same time in many instances the radial pores are widely spaced. In no case is there any indication of the presence of cellulose bars of Sanio, although many of the specimens, which have passed under my notice are in a remarkable condition of preservation, which has been a matter of comment on the part of all who have examined them.

Figure *c*, Plate 7, illustrates part of a transverse section of *Arau-*

cariopitys americana [35] showing a series of traumatic resin canals. The row nearer the center of the stem is larger and better developed, while that farther out is composed of very small canals separated by wider intervals. As has been pointed out in the article cited above, the traumatic resin canals in Araucariopitys are more nearly like those of the Abietineae, than is the case with canals of this type which have been described in any other American wood of Araucarian affinities. In Araucariopitys the rays too are distinctly of the Abietineous type, being composed of thick-walled cells, strongly pitted. The radial bordered pits of the tracheids however are often arranged in the compressed and sometimes in the alternating manner of the Araucarian conifers. Moreover there are no bars of Sanio present, although much of the material on which the genus Araucariopitys has been founded is in a perfect condition of preservation. Gothan, as has been indicated in the earlier paragraphs of this article, has described woods of a similar type from the Jurassic beds of King Carl's Land and Spitzbergen. These have traumatic resin-canals, thick-walled and strongly pitted ray cells. This author does not figure the presence of bars of Sanio in these woods of the arctic regions, so that it may be assumed that they are absent as in Araucariopitys, especially as woods of a similar horizon and identical features of organization, which I have examined, show no indication whatever of these peculiar structures, which constitute transverse bands between the radial pits of the tracheids, in all coniferous except Araucarian woods. Miss Gerry has investigated the distribution of bars of Sanio in the Coniferales in a comprehensive manner and found them to be absent in all Araucarian woods, living or extinct, which she examined.[36] Before discussing the conditions found in the Araucariopitys type, it will be well to consider briefly woods of a similar type from older geological horizons. It is pertinent before doing this, however, to point out that the Araucariopitys type, so far as our present knowledge goes, is rare in the later Mesozoic (*i. e.*, the Cretaceous).

Figure *d*, Plate **7**, shows the presence of two rows of resin canals of the traumatic type in an Araucarian wood from the Upper Jurassic. This wood and others of the same type will be described in detail on another occasion. At the present time only those features, which are of importance in the present connection, will be dealt with. The section from which Figure *d*, Plate **7**, was made, shows a distinct wound cap a few annual rings away from the pith. From this on either side

[35] Jeffrey, Bot. Gazette, **44**, pps. 435–444.
[36] Distribution of Bars of Sanio in the Coniferales, Ann. Bot. **24**, pp. 119–124.

extend rows of wound resin canals. Farther out these disappear entirely as is wont to be the case in woods, giving rise to canals of this type, unless the injury is extremely severe. The canals are in some cases obviously very wide in the tangential plane. This feature indicates their lateral fusion with one another, a condition quite typically present in traumatic resin-canals. The canals are surrounded by cells filled with very dark contents, which sometimes makes its way into the lumen of the canal itself. The rays are likewise occupied by a dense dark hued substance. Figure *e*, Plate 7, shows the canals in longitudinal radial section. They are clearly not of equal caliber throughout as is usually the condition in Pinus, but are constricted at intervals even in the short portion shown in the figure. This condition is likewise one, which is characteristic of traumatic resin canals, although it is also more or less observable in the normal canals of the wood in the Abietineous genera, Picea, Pseudotsuga and Larix. To the right and left of the resin canal are medullary rays. The magnification is not sufficient to show their structure, which will be figured in detail subsequently. It is enough to state that the rays in this region of the wood are very strongly pitted, exactly as in Araucariopitys described above. The pitting is Araucarian of the Brachyoxylon type, that is the pits are not only flattened or alternating but also occur in the rounded and well spaced condition characteristic of the Conifers, other than the Araucarian tribe. Bars of Sanio cannot be made out in the wood under consideration or in any similar ones from the same deposits.

It is clear from the foregoing paragraph that there are woods in the Jurassic, which as regards their features of organization combine Abietineous and Araucarian characteristics. They have namely the strongly pitted rays and traumatic resin canals of the Abietineae, combined with the pitting of the tracheids and the absence of bars of Sanio which are recognized, by those who have made a special study of Araucarian woods, as diagnostic of the Araucarian tribe. There are obviously two possible interpretations of the combination of characters referred to above. It is agreed by competent investigators that the features under discussion clearly indicate a close degree of relationship in the Jurassic, between the Abietineous and Araucarian tribes. The disagreement, however, arises as to whether the Abietineae have come from the Araucariineae or the opposite mode of derivation is the correct one. Gothan in the two important memoirs on the Jurassic woods of King Carl's Land and Spitzbergen cited above, takes the view that the transition is from the Araucarian

Conifers to the Abietineae and bases his position on the structure of the rays, which he claims is the most trustworthy diagnostic character of coniferous woods. That is a view to which the present writer cannot subscribe, as from an extended comparative, anatomical, developmental, experimental, and paleobotanical acquaintance with coniferous woods he is in the position to state that wide variations of ray structure occur within all the coniferous tribes, and that as a consequence this feature of the organization of the wood cannot be successfully employed for the diagnosis of the woods of extinct conifers. It has been pointed out in the first article of this series, that even in so highly specialized an Araucarian species as *Agathis australis*, rays of the Abietineous type occur normally in the wood of the cone and may be readily produced traumatically in the wood of the root. A similar illustration may be cited in the case of Sequoia. As is well known the rays in the Sequoiineae are usually composed of thin walled cells without intercommunicating pits. In the cones of both the living species of Sequoia, particularly *S. gigantea*, the cells of the rays of the woody axis are very strongly pitted, especially towards the primary wood. Further in this genus strongly pitted rays appear as the result of injury. It appears quite clear from the conditions in the case of *Agathis australis* and *Sequoia gigantea*, that ray structure may vary greatly within the same genus and even the same species and consequently cannot be as an infallible diagnostic feature. The presence of rays of the Abietineous type consequently cannot be taken as satisfactory proof that the Jurassic woods under discussion are in reality Abietineous. This consideration likewise applies to the presence of traumatic resin canals because if these alone were a sufficient diagnostic character, we would be compelled to put the wounded wood and normal cone axes of *Sequoia gigantea* under the Abietineae, although the sum of characters of that species by common consent justify the placing of it in an entirely distinct tribe. Let us now turn to more constant characters than ray structure or traumatic resin-canals, namely the pitting of the tracheids which has been admitted by all experts, with the sole exception of Dr. Gothan, as an important Araucarian diagnostic feature. In the Jurassic woods under discussion the radial pitting of the tracheids is distinctly of the Araucarian type. Further we have recently had added to the list of utilizable diagnostic characters of Araucarian woods, the absence of the cellulose bars of Sanio, as worked out by Miss Gerry.[37] True

[37] *Op. cit.*

Gothan has stated that the absence of bars of Sanio is to be explained by the close approximation of the radial pits in the tracheids of the Araucarian tribe. It has been shown however that in the seedling, cone-axis and leaf trace of the living Araucarian conifers the pitting is not crowded as is the case in the mature secondary wood of the trunk and root. This is particularly true of the base of the seedling stem, where typical Araucarian pitting appears only after many years. In spite of the free spacing of the pits of the tracheids in the regions just described bars of Sanio are absent, *except in the part of the secondary wood of the cone axis, immediately adjoining the primary xylem*, as has been indicated in the second article of the present series. It follows apparently that Gothan's explanation of the absence of the bars of Sanio in Araucarian woods is not the valid one. On the criteria of the absence of bars of Sanio and presence of Araucarian radial pitting, the Jurassic woods under discussion are clearly of Araucarian affinities. Moreover if we admit for the sake of argument that the Jurassic woods in question are Abietineous, what is to become of the very numerous woods of the Cretaceous of the Brachyoxylon type, which have traumatic resin canals but have not normally at least the strongly pitted rays of the Abietineae? They can scarcely be included on the basis of Gothan's view with the Abietineae on account of their not possessing his sovereign diagnostic, Abietineous ray structure. Professor Seward has agreed that woods of this type are "undoubtedly Araucarian" and it may be assumed that such is the case until serious argument to the contrary can be adduced.[38]

Gothan in his articles cited above, has to assume that practically all the coniferous woods of the high arctics are Abietineous in their affinities, thus leaving no woody structures for the numerous Araucarian conifers, which are known to have flourished in that period. Moreover if we grant his identification of Jurassic woods with strongly pitted rays, traumatic resin canals, Araucarian radial pitting and non existent bars of Sanio, as of Abietineous affinities and indicating a recent derivation of the Abietineae from Araucarian ancestors, what shall we say of the characteristic Cretaceous woods of the Brachyoxylon type, which resemble these in every respect except in the absence of the Abietineous type of ray? If we derive the Araucarian conifers from the Abietineae no such difficulty arises, because we would expect on such an hypothesis, to find the Araucariineae progressively less like the Abietineous stock in later geological time. On the basis of

[38] The Araucarieae, Recent and Extinct, Phil. Trans. Roy. Soc. London, Series B. **198**, p. 382.

ray structure alone then we find that the woods which as the result of the consideration of their most reliable diagnostic features are Araucarian, form a logical sequence on the hypothesis of derivation from the Abietineae, from the earlier to the later Mesozoic (Jurassic and Cretaceous). The opposite hypothesis, even taking into consideration the ray structure only, apparently involves us in hopeless confusion.

Having considered the known types of fossil Araucarian woods in regard to the feature of the presence or absence of resin canals, it is now desirable to inquire whether there is any evidence for the normal or traumatic occurrence of resin canals in the wood of existing representatives of the Araucariineae. In this connection the writer has had somewhat exceptional opportunities of securing material. Through the kindness of the late Director of the Botanic Gardens of the Dutch Government at Buitenzorg, Java, an abundant supply of the Malayan representatives of the genus Agathis were secured, including all vegetative parts of the plant, together with the very important cones. Later Dr. Maiden of the Botanic Gardens in Sydney, N. S. W. Australia, and Dr. Baker of the Technological Museum, Sydney, have forwarded abundant material of Australasian and exotic species of Agathis and Araucaria. The writer is likewise indebted to his students, Dr. A. J. Eames and Mr. E. W. Sinnott for collections made in Australia and New Zealand, secured in connection with their tenure of Sheldon Traveling Fellowships of Harvard University. The latest contribution to the writer's stores of valuable material was supplied through the kindness of the Director of the Royal Garden, Kew, England, and through the goodness of Mr. L. A. Boodle of the Jodrell Laboratory, Kew. It should be emphasized here that the abundant material, which has been secured through the kindness of many botanists, covers all the anatomically interesting parts of the two living genera of the Araucariineae and to a remarkable extent their whole geographical range. Not only has normal material been available but also that which has through injury or other causes undergone abnormal development.

It is the writer's purpose to give an account of the organization of the cone of the Araucarian conifers, in its systematic and anatomical aspects in an article distinct from the present series. Only features of special interest in the present connection will be considered here. As a preliminary to a description of these features, a general statement may be made in regard to features of organization of the ovulate strobilus, of importance in the case of this investigation. The writer has

found, in those species of Araucaria, which have both the upper and lower systems of fibrovascular bundles present in the cone-scales of their ovulate strobilus, that the axial region of the cone does not show certain remarkable features found in the case of those species in which the upper system of cone-scale bundles has disappeared. In the latter condition there are apparent medullary resin-canals present in the pith of the cone axis. In the lower region of the cone these resin-canals are often surrounded with the tissues of the xylem, which constitute medullary strands joining with the wood of the cylinder of the axis, at the points where the supply of the cone-scales is given off. Without going into the matter here it may be stated that the medullary strands, containing resin canals in certain species of Araucaria and Agathis represent the vanished upper system of cone-scale bundles. The wooden envelope of the resin-canals disappears in the upper region of the cone and is best developed in the peduncular region. In Agathis, only the most primitive species have the medullary vascular strands. In the case of *Agathis Bidwillii*, resin-canals are found not only in the wood of the medullary system of bundles but they likewise not unfrequently make their appearance in the bundles of the lower cone-scale series, which are alone present in this genus. This feature is shown in Figure *f*, Plate **7**, which represents a cone-scale supply in the lower region of the cone, passing out through the wood of the axis. In the upper region of the scale supply and immersed in the elements of the primary xylem, is to be seen a dark mass which represents a resin canal filled with mucilaginous contents, a common accompaniment of the resinous secretion both in Agathis and Araucaria, as well as in the resin passages of extinct representatives of the Araucarian stock. Mucilage is particularly abundant with the resin in the canals of Agathis. The peculiar position of the resin canal in the primary wood, is to be compared with the conditions in living and extinct pines, where the first formed resin canals are often embedded in the elements of the primary wood. The present writer has described similar conditions in the case of the vestigial resin-canals of the cone-axis and cone-scales of the genus Sequoia.[39] Interesting in this connection are likewise the resin canals in the primary wood of the root in the two subtribes of the Abietineae, the Pineae and the Abieteae. The occurrence of resin canals in the outgoing vascular supply of the cone-scales on *Agathis Bidwillii* is an extremely incon-

39 Jeffrey, Comparative Anatomy of the Coniferales. I. The genus Sequoia, Mem. Boston Soc. Nat. Hist. **5**.

stant feature and shows various stages of degeneracy the canal often for instance being largely or even wholly blocked with tyloses.

The occurrence of resin-canals in the scale bundles in a species of Agathis is a feature of considerable interest phylogenetically. The question at once arises whether it is to be regarded as an inchoative stage in the development of resin canals in the group or a vestigial one. Its place of origin appears to negative the former hypothesis. We may in fact compare the occurrence of vestigial resin-canals in the xylem strands of the peduncle of the cone in Agathis Bidwillii, with the development of vestigial centripetal wood in the peduncular region of the cone of certain Cycads, the very interesting and important discovery of Dr. Scott[40] or the existence of the same ancestral type of xylem development in the strobilar organs of Equisetum, long after it has disappeared in the vegetative axis of the ancient stock from which that genus has been derived.[41] The resin-canals in question are also to be regarded as ancestral on account of the wound reactions of Mesozoic Araucarian woods, which have been discussed above. These interesting vestigial resin-canals appear in the vascular supply of the lowermost abortive cone-scales, attached to the peduncle of the cone, and die out before the cone-scale supply leaves the wood of the peduncular axis. They have as yet been found only in *Agathis Bidwillii*. It does not appear at all likely that they will be discovered in other living species of the genus Agathis. It is probable on other grounds, that this species is the most primitive now in existence.

It naturally has occurred to the writer to investigate the wound reactions of the stem and roots of living species of Agathis and Araucaria. The results of extensive examinations of wounded material from the Australasian and East Indian regions have however been entirely negative. There is reason to suppose however from a series of investigations carried on with another purpose that traumatic reactions in the seedlings, particularly the seedlings of *Agathis Bidwillii*, may yield more favorable results, since it has been found in certain instances that seedlings respond much more readily to experiment than does the adult plant. It seems clear that so far as the mature individuals are concerned, however, that the living representatives of the Araucarian stock have entirely lost their capacity for producing reversionary wound resin canals, and in this respect as in other equally important normal features of structure, differ from a

40 Scott, D. H., The Anatomical Characters of the Peduncles of Cycadaceae, Ann. Bot. II (1897).

41 Eames, Centripetal Xylem in Equisetum, Ann. Bot. **23**, (1909).

large number of Araucarian forms, which apparently became extinct with the close of the Mesozoic.

As a consequence of the investigation of the normal and traumatic occurrence of resin canals in the wood of the Araucariineae, living and extinct, the conclusion seems clear, that this tribe of conifers once possessed ligneous resin canals as a normal feature and there is thus added one more argument for deriving them ancestrally from the Abietineae and not directly from the Cordaitales, as is commonly held. This view of the matter is strongly supported by the data described in the previous article, in connection with the pitting of the tracheids and the distribution of bars of Sanio. It is likewise confirmed by the evidence as to the ancestral character of the ray structure in the Araucarian tribe, which strongly resembled that found in the Abietineae, past and present. The ancestral occurrence of wood parenchyma in the Araucarian tribe is likewise a strong argument against their immediate connection with the Cordaitean forms and indicates that they in common with the conifers in general, with diffuse wood parenchyma are of relatively recent origin compared with the Abietineae, which in so many ways show themselves to be a very ancient group.

Summary.

1. Certain Mesozoic woods from the Jurassic and Cretaceous, showing traumatic resin canals are of Araucarian affinities.

2. This is shown to be the case by the structure of their tracheids, both as regards pitting and the absence of cellulose bars of Sanio.

3. Abietineous pitting in the rays of extinct conifers is not in itself a character of sufficient constancy to serve as a reliable diagnostic feature, since pitting of this type can readily be produced as the result of injury and moreover is often normal in the more conservative parts of living representatives of the Araucariineae.

4. Normal resin canals occur embedded in the primary xylem of the traces leading to the abortive cone-scales attached to the peduncular region of the cone of *Agathis Bidwillii*.

5. This fact taken together with the traumatic phenomena presented by certain Mesozoic Araucarian woods, supplies an additional argument for the derivation of the Araucariineae from an Abietineous ancestry.

PLATE 7.

Fig. *a*. Transverse section of the wood of *Brachyoxylon notabile*, showing wound resin canals. × 40.

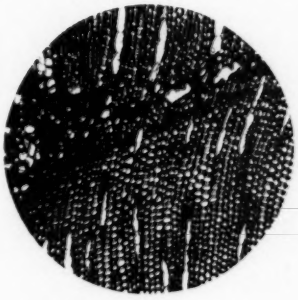
Fig. *b*. Another section of the same showing traumatic resin canals more remote from the wound. × 40.

Fig. *c*. Transverse section of the wounded stem of *Araucariopitys americana*, showing wound resin canals. × 100.

Fig. *d*. Transverse section of a wood from the English Jurassic, showing traumatic resin canals. × 40.

Fig. *e*. Longitudinal section of the same. × 40.

Fig. *f*. Tangential section through the wood of the peduncle of the cone of *Agathis Bidwillii*, showing the presence of a normal resin canal in the vascular supply of the cone-scale. × 100.



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THE HISTORY, COMPARATIVE ANATOMY AND EVOLUTION OF THE ARAUCARIOXYLON TYPE.

By Edward C. Jeffrey.

Part IV.

The present article will be devoted to the consideration of the structure of the pith and the relations of the foliar trace in woods of the Araucarioxylon type and nearly allied Araucarian lignites. Gothan in his second memoir on arctic woods, which deals with the fossil ligneous remains of the island of Spitzbergen, makes the statement that the Cretaceous fossil, which the present writer has described under the name Araucariopitys [42] and considered on the basis of its general organization to belong to the Araucarian alliance, cannot be so referred on account of the abietineous character of its rays and on account of the sclerotic septa in the pith, a character in his opinion likewise exclusively Abietineous.[43] The writer has shown in the first article of the present series, that the presence of Abietineous rays is by no means necessarily an indication of Abietineous affinity, especially in the case of Mesozoic woods. It will be his aim to demonstrate in the present communication that sclerotic diaphragms in the medullary region are equally fallacious criteria of Abietineous affinities. Professor Seward has adduced the persistent leaf trace of the living genera Agathis and Araucaria and of true Araucarioxyla from the Mesozoic deposits, as an argument for the antiquity of the Araucariineae and for their relationship with the extinct Lycopodiales, which he considers likewise as characterized by leaf-traces persistent for a long time in the secondary wood. The writer will attempt to show in the present article that on generally accepted biological principles the leaf trace was not

42 Jeffrey, Araucariopitys, a new genus of Araucarians, Bot. Gazette **44**, pp. 435–444.

43 Gothan, Die Fossilen Holzreste von Spitzbergen, Kung. Svensk. Vetenskap. Handlingar, Bd. 45, No. 8, Uppsala u. Stockholm (1910).

primitively persistent in the Araucarian stock and consequently cannot be used as an argument for their antiquity or their affinity with any other group in which the persistence of the foliar strands is a feature of structure in the wood.

Figure *a*, Plate 8, illustrates a transverse section of a well preserved Araucarian trunk from the Raritan Cretaceous of Kreischerville, Staten Island, N. Y., which has been described by the author under the name *Araucarioxylon noveboracense*.[44] Through the center of the figure vertically passes the leaf trace. The annual rings are scarcely curved at all, showing that the stem was one of considerable thickness, its age in fact being somewhat over fifty years. This persistence of the leaf trace seems to be a characteristic of all woods of the true Araucarioxylon type and as has been particularly indicated by Dyer [45] and Seward,[46] is likewise a feature of the trunks of the living genera Agathis and Araucaria. Throughout the wood of the figure may be seen numerous dark dots, indicating the position of the true resiniferous parenchyma, which as has been pointed out in the first article of this series, seems to have been a constant feature of structure in the true Araucarioxyla of the Mesozoic, and which interestingly enough persists as a vestige in the wood of the cone, first annual ring of vigorous branches and the root of the living genera Agathis and Araucaria. Woods of the Araucarioxylon type in the stricter sense, have been described recently by Lignier from the Middle and Upper Jurassic of France.[47] They are exceedingly common in the Cretaceous both of Europe and America.

In addition to the true Araucarioxylon type, there exist, particularly in the Cretaceous, woods in which the pitting and general structure of the tracheids, although unmistakably Araucarian, present certain features of divergence from those properly included under the generic appellation Araucarioxylon. These are pitting not invariably flattened or alternating and the presence of wound resin canals in connection with injuries. These woods are further characterized by rays which are frequently of the Abietineous type after injury. Another interesting feature of these woods is the fact that the leaf-traces, instead of being persistent as is the case with the living genera Agathis and Araucaria, endure only for a very short

44 Hollick and Jeffrey, Cretaceous Coniferous Remains from Kreischerville, Mem. N. Y. Bot. Garden, 3.

45 Persistence of Leaf traces in Araucarieae, Ann. Bot. 15, pp. 547 (1901).

46 *Op. cit.*

47 Lignier, Végétaux Fossiles de Normandie, IV. Bois Divers, Ire. Série, Caen (1907).

time, a few years at most. The writer has discussed and figured woods of this type in a memoir on the Coniferous remains found at Kreischerville, Staten Island.[48] It is accordingly unnecessary to do more than call attention to their characteristic features here. It has been pointed out in the second article of this series that peculiarities of pitting and other features, found in Mesozoic woods of this type, to which the writer has given the generic name Brachyoxylon, are likewise found in the seedling axis and the cone axis of the living genera, Agathis and Araucaria. In Agathis the Brachyoxylon type of pitting persists for very many years in the basal region of the seedling. It has occurred to the writer that since the older less typically Araucarian mode of pitting persists in the seedlings and cones of the living genera of the Araucarian conifers, that the evanescent leaf traces, which are likewise a feature of the Brachyoxylon type of wood as contrasted with the persistent ones of the Araucarioxylon type, might be found in the seedling axis of Agathis and Araucaria, in accordance with the general biological law of recapitulation. An examination of the facts resulted in a very gratifying realization of this theoretical expectation. Figure *b*, Plate 8, shows a tangential section through the epicotyledonary region of the seedling stem of *Agathis australis*, material of which was obtained by Messrs. Eames and Sinnott, Sheldon Traveling Fellows of Harvard University, on a journey to the Australasian region. In the center of the figure are seen two leaf traces in transverse section. Of these one is better developed than the other. The smaller one is about to disappear. Figure *c*, Plate 8, shows a section of the same stem a little farther out. The trace which shows smaller in Figure *b*, has now completely disappeared and the persistent one has become much reduced in size. A serial examination of sections showed that the leaf trace came off as a single strand from the region of the protoxylem of the stem and after passing out a very short distance divided into two. The double strand thus produced is of very short duration and finally disappears in both its divisions in the third or fourth annual ring. As one passes up the seedling stem, the leaf traces are seen to become more and more persistent until they reach a condition of permanency like that characteristic of the older stem. It is clear from the facts described that the leaf trace of Agathis, so far as *A. australis* is concerned at any rate, in the seedling is an evanescent structure and only becomes permanent later in life. The conditions are comparable in fact *mutatis mutandis*, with the conditions found

[48] Hollick and Jeffrey, Coniferous Remains of Kreischerville, Mem. N. Y. Bot. Garden, 3.

in the seedling of our only deciduous occidental conifer the larch, for here in the seedling the leaves are persistent for two or three years and only gradually become annually deciduous. There can be no doubt that in the case of the larch we have to do with a tree, which originally had evergreen leaves, as is the case with the other conifers, and that its seedling perpetuates that condition. *Vice versa* in Agathis we have to do with a coniferous genus, which originally had its leaves moderately persistent as in conifers in general and that only later did the extreme condition of persistence of the leaf trace found only among living conifers in the mature stems and lateral branches of the genera Agathis and Araucaria, become established. It is to be emphasized then as a result of the examination of the seedling anatomy of Agathis that not only the pitting of the older Mesozoic type Brachyoxylon persists in the seedlings of the living genera but also the evanescent character of the foliar trace. Seedlings of *Araucaria Bidwillii* were examined with similar results, the only difference being that the leaf traces here are somewhat more persistent in the lower region of the cotyledonary stem than they are in Agathis. It appears unnecessary to furnish further illustrations, since the facts seem to be so conclusive and so much in accord with the natural theoretical expectation.

Having made it clear that both the anatomical conditions found in the older Mesozoic woods of Araucarian affinities (Brachyoxyla) and the developmental data supplied by the seedlings of the modern forms, vouch for the fact that the persistent leaf trace characteristic of the woody cylinder of the living genera of the Araucariineae and of woods of a similar type from the Mesozoic, (true Araucarioxyla) is not an ancestral feature of the stock, and consequently not phylogenetically important, we may appropriately pass on to the consideration of the pith in the primitive Araucarian type, in connection with the affinities of the Araucarian stock.

Figure *d*, Plate 8, illustrates the structure of the pith in the stems, the wood of which has been described by the author under the appellation *Araucarioxylon noveboracense*.[49] At quite regular intervals the pith is characterized by the presence of lighter bands, which represent regularly recurring transverse diaphragms of sclerotic tissue. Figure *e*, Plate 8, illustrates the same feature in the pith of an undescribed and different species of Araucarioxylon from the Raritan Cretaceous of Cliffwood, New Jersey. Sclerotic diaphragms appear at intervals

[49] *Op. cit.*

in the pith and often occupy a somewhat oblique position. Figure *f*, Plate **8**, shows a portion of one of these somewhat more highly magnified. The contrast between its organization and that of the ordinary tissues of the pith can clearly be made out. In the memoir on the Conifers of Kreischerville, the writer has called attention to the very frequent occurrence of medullary septa of a sclerotic nature in the pith of branches not only of the Brachyoxylon type, but also of the probably still older type, to which the name Araucariopitys has been applied. It is interesting to consider the organization of the pith in the two Cretaceous Araucarioxyla described above. They have the same tendency to form sclerotic diaphragms. Gothan in a recent memoir on the fossil woods of Spitzbergen [50] has questioned the accuracy of the writer's reference of the genus Araucariopitys to Araucarian rather than to Abietineous affinities, because he thinks it impossible that an Araucarian conifer should have the pith structure and ray structure, which so far as living representatives of the Coniferales are concerned is more characteristic of the Abietineae than of the Araucariineae. It is clear that conclusions as to affinities can only be safely drawn after a full and accurate comparison of Mesozoic and living forms. Most of the results of structural paleobotany, in the case of Mesozoic conifers at any rate, are vitiated by a neglect of this absolutely necessary precaution.

The writer has not observed the presence of true sclerotic diaphragms in either the seedling stem or the cone-axes of any living Araucarian species. Isolated stone cells are typical of Araucaria, and sclerotic nests which never become so extensive as to constitute true diaphragms are found in Agathis.

It appears to be definitely established from the data supplied in the present article that persistent leaf traces cannot in the future be regarded as an infallible diagnostic of Araucarian woods. It seems further clear that foliar traces of this type are not a primitive feature of Araucarian woods, since they are not characteristic of the seedling structure of living representatives of the Araucariineae, and are not found, in what we must regard on the basis of a great many concurrent lines of evidence, as the older Araucarian types, namely Brachyoxyla and woods of the organization of Araucariopitys. It is moreover obvious that medullary diaphragms are equally characteristic of both the older Araucariineae and of the Abietineae living and fossil. Their presence in older Araucarian types, is consequently one more piece

50 *Op. cit.*

of evidence in favor of the derivation of the Araucarian tribe from Abietineous ancestors.

Having in the present article and those which have preceded it, considered a number of anatomical features presented by the Araucarioxylon type and by the living genera with the same type of wood, we are in a position to discuss its affinities and evolutionary development. It has been pointed out in the first article that there is the best of evidence, derived from both fossil and living forms, that woods of the Araucarioxylon type were originally characterized by the possession of strongly pitted rays and abundant wood parenchyma. These features are quite inconsistent with a direct connection of this type with the Cordaitean plexus of gymnosperms, since here, we know, that the wood was entirely without wood parenchyma and the rays were composed of cells with unpitted walls. Passing to the next important item of wood structure, we find that there is every reason to believe that the older Araucarian conifers were not characterized by alternating or compressed pitting. On the contrary the radial pits were often opposite and moreover were separated from one another, particularly towards the ends of the tracheids, by cellulose bars imbedded transversely in the lignified wall of the tracheids. Bars of this type do not occur in any Cordaitean woods but are found in the mature wood of all existing Conifers, *except the living Araucariineae.* It follows that on the basis of pitting and the cellulose bars of Sanio, the Araucarian conifers were derived from the same ancestors as the remaining coniferous tribes. It is further clear both from a consideration of comparative anatomy and from the organization of the older woods belonging to the Araucariineae, that the absence of resin canals is not a primitive feature of Araucarian woods, since the progenitors of the stock clearly possessed them. The present article appears moreover to make it clear that persistent leaf traces are not an ancestral feature of organization of the Araucarian stock, both the anatomical conditions found in the older forms and in the seedlings of the living genera, showing beyond any reasonable doubt, on generally accepted biological principles, that the leaf strand in the ancestors of the Araucarian stock, persisted only for a few years, as is characteristically the case in all other living conifers.

It is apposite to consider if other facts justify the conclusion reached in connection with the present investigation, namely that the Araucarian stock is distinctly coniferous and is neither the most ancient tribe of the Coniferales, nor connects them with those ancient Gymnosperms, which the majority of competent morphologists regard as

the ancestors of the coniferous stock, namely the Cordaitales. Taking first the very important criterion from the standpoint of the systematic arrangement of the Coniferales, the organization of the female cone, we find little to justify the recent contention of Professor Seward and his students and of Mr. Thomson, that the ovulate cone of the Araucarian conifers is of a different morphological order from that characteristic of the remaining coniferous tribes. It is perfectly clear that not only in the more primitive species of the living genus Araucaria but also in the cones of the Mesozoic representatives of the Araucariineae, described by the present writer either independently or in collaboration with Dr. Arthur Hollick, that the Araucarian female cone, like that of the other tribes of conifers was originally composed of cone-scales with a double system of bundles, independently emanating from the cone axis and of inverse orientation. Consequently whatever explanation is adopted for the double system of bundles in one case must be adopted in all. Attempts to read the Araucariineae out of the conifers must continue so long as the view is adhered to that they represented the primitive elaboration of the coniferous stock. It is a noteworthy fact that Professors Penhallow and Seward as well as Mr. Thomson, who much as they disagree in other matters are in harmony in regarding the Araucariineae as distinct from other coniferous tribes and at the same time as the primitive representatives of the stock. The recent investgations of Mr. A. J. Eames [51] appear to make it perfectly clear that whatever explanation is adopted of the organization of the female strobilus in the Araucariineae, must hold likewise for all the remaining tribes of Conifers.

If we turn our attention now to the gametophytes, we arrive at similar conclusions, if our logical processes are based on the established principles of biological science. Taking first the male gametophyte, we find a method of germination of the microspore unlike that found in any other gymnospermous group, which has been inaptly denominated by Mr. Thomson as 'protosiphonogamic.' Certainly we would not expect to find the primitive type of pollen tube formation in a group in which the pollen no longer reaches the apex of the ovule, as it characteristically does in all other known groups of Gymnosperms, living and extinct. The peculiar germination of the pollen of Agathis and Araucaria, on the cone scale and not on the apex of the young seed is an unmistakable stigma of aberration. The contents of the pollen tube likewise vouch for the highly specialized con-

51 Ann. Bot. *Ined.*

dition of the Araucariineae. Here the two prothallial cells common to the Abietineae and the equally ancient Ginkgoales become proliferated into a large number, doubtless in correlation with the extreme length and meandering course of the fertilizing tube. Moreover the absence of a stalk cell in connection with the setting off of the body cell, which gives rise to the two sperm cells, is a clear and outstanding feature of aberrancy. Mr. Eames in the memoir, already cited, has shown moreover, that in the organization of the female gametophyte, the structure of the archegonium, the nature and functions of the archegonium neck, as well as in the method of penetration of the pollen tube and the development of the embryo, the Araucarian conifers manifest not a primitive but an extremely aberrant condition. They are in fact comparable to a large degree in their systematic position with the edentate fauna, likewise characteristic of the antarctic region, Developmental investigations on the zoological side have recently shown that the edentulous features which have been until the present time regarded as a primitive feature of this group are in reality marks of aberrancy, since a more abundant dentition, at first makes its appearance in the embryo.

Reviewing all the evidence in the light of many recent investigations both in general morphology and in the morphology of the conifers in particular, it is clear that it is the anatomical features of the reproductive and vegetative organs, which give us the most reliable criteria as to the evolution of the coniferous stock and above all in the present connection, as to the evolution of the Araucarian tribe. The anatomical conditions in the living forms cannot be understood without careful comparison with the organization of those which are now extinct. Basing our conclusions on these criteria, the result is reached that the Araucarioxylon type has been derived from the Pityoxylon type and as a consequence formerly possessed the opposite pitting, the bars of Sanio, the strongly pitted rays and the resin canals of the ancient Abietineous woods. Some of these characters are still to be observed in primitive regions of the existing Araucariineae, while others are to be inferred from a consideration of the organization of Araucarian forms now extinct. It is further clear that the external form of the reproductive structures and the organization of the gametophytes supplies as little light, regarded independently from the anatomical organization of the reproductive and vegetative parts, for the interpretation of the true course of evolution and affinities of the ancient but highly aberrant coniferous tribe, the Araucariineae as is the case with the corresponding structures in the Bennettitean

tribe among the Cycadophyta. It is finally clear that morphologists will find it necessary in the future more and more to adopt certain general working principles, as in the case for example in the sister sciences of chemistry and physics. If there prove on trial to be no generally applicable fundamental principles in morphology, that branch of biological science cannot be too soon cast into the outer darkness, which prevails outside the scientific view of nature.

General Conclusions.

1. The Araucariineae cannot have been derived from the Cordaitales since they possessed primitively a number of features which so far as our knowledge goes, never existed in the Cordaitean stock.
2. The Araucarioxylon type is derived from ancestral forms, which possessed opposite pitting, bars of Sanio, strongly pitted rays and horizontal and vertical resin canals.
3. The primitive existence of these features in the ancestral type from which Araucarioxylon has been derived, show clearly that it has taken its origin from the Abietineous Pityoxylon type.
4. This conclusion is entirely confirmed by a consideration of the reproductive structures both sporophytic and gametophytic.
5. Any hypothesis as to the origin of the Coniferales in general must start with the Abietineae as the most primitive tribe.
6. It is absolutely essential to the progress of plant morphology, that investigation be carried on in connection with the elucidation of the general working principles of the biological sciences.
7. The comparative, developmental, paleobotanical and experimental investigation of the Coniferales is likely to throw more light on the stable and sound general principles of biology, than that of any other large group of animals or plants, on account of their great geological age and remarkably continuous and complete display, both as regards external form and internal structure in the strata of the earth.

Botanical Laboratories of Harvard University,
17th, June, 1912.

PLATE 8.

Fig. *a*. Transverse section of the wood of *Araucarioylon noveboracense*, showing the persistent leaf trace. × 15.

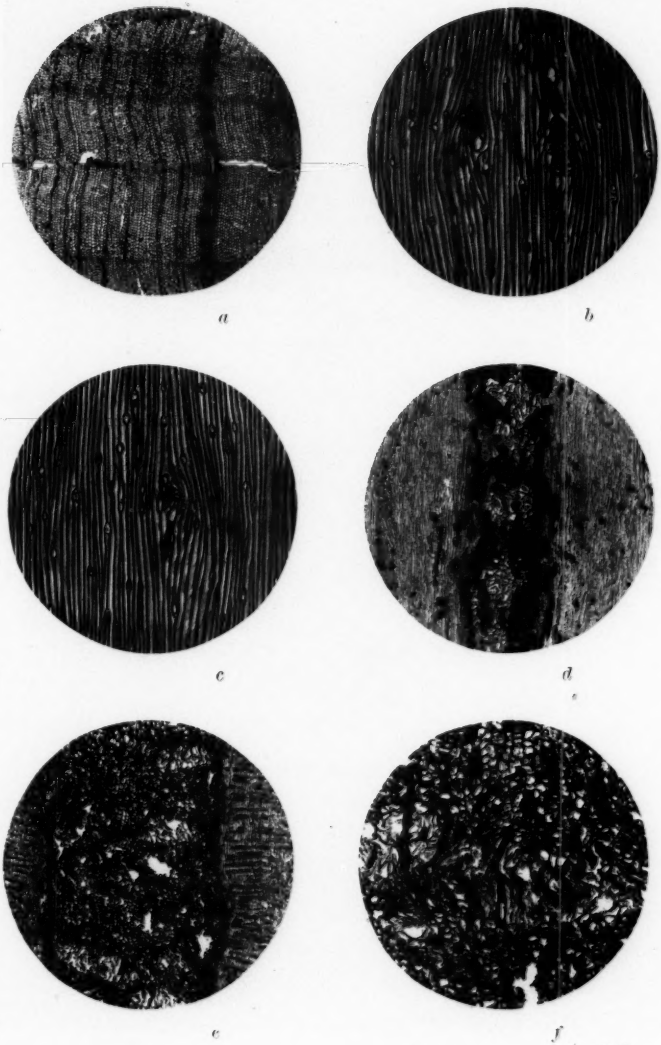
Fig. *b*. Tangential section of the seedling stem of *Agathis australis*. × 60.

Fig. *c*. Another of the same further out in the wood. × 60.

Fig. *d*. Longitudinal section through the pith of a trunk of *Araucarioxylon noveboracense*. × 8.

Fig. *e*. Longitudinal section of an undescribed species of Araucarioxylon from New Jersey, showing the region of the pith. × 15.

Fig. *f*. Part of the same more highly magnified. × 40.



a *b*

c *d*

e *f*

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